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**CHIROTHERIUM LULLI, A PSEUDOSUCHIAN REPTILE
FROM NEW JERSEY**

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INTRODUCTION

In 1885 the vertebrate paleontologist and bibliographer John Eyerman, while examining Upper Triassic exposures in the Delaware River valley, discovered fossil footprints in the quarries of the Messrs. Clark near Milford, Hunterdon County, New Jersey. The series of footprint-bearing slabs which he collected was deposited in the geological museum of Lafayette College at Easton, Pennsylvania. Aside from a brief notice of the discovery by Eyerman (1886), curiously superficial descriptions of some of the species by C. H. Hitchcock (1889), and a redescription of *Chirotherium* [*Otozoum*] *parrum* by Lull (1904, 1915), the Lafayette footprint collection received little attention for 65 years. Recently Wilhelm Bock, while preparing a general treatment of Triassic reptilian tracks from the Newark basin of New Jersey and Pennsylvania, re-examined the collection and made good the previous neglect by describing and figuring the significant specimens. One of these, a small manus-pes set impressed in reddish-brown siltstone, became the type of the new species *Chirotherium lulli* Bock (1952).

During the same period a convergent series of events took place. An amateur fossil collector acquired (perhaps at an auction) a fine slab of fossil footprints reported to have come from Sanatoga, Pennsylvania. This slab of reddish-brown siltstone bore in relief the casts of four successive small tracks, the last overlapped by the birdlike footprint of a dinosaur. After the owner's death the slab was fortunately obtained for the Academy of Natural Sciences of Philadelphia by Wilhelm Bock, too late however for inclusion in his paper, and after the type of *Chirotherium lulli* had been returned to Lafayette College.

At this point, in the course of preparing a faunal study of the Milford reptile footprints in the Museum of Comparative Zoology, I visited Philadelphia and Easton and made latex molds of both specimens. On comparison of the molds it immediately became evident that, although the specimens are labeled as having come from different states, the type of *C. lulli* is the counterpart of the third manus-pes set on the Philadelphia slab. Every detail of the footprints and every furrow, rain-print, and exfoliated patch on the surface of the slabs corresponds exactly.

From this excellent new material so fortuitously brought to light we may draw a more precise understanding of the morphology and relationships of *Chirotherium lulli*. Its peculiar combination of primitive and advanced characters, its association with ornithoid dinosaur footprints, its bearing on problems of stratigraphic correlation, and its position as the youngest known member of an important genus justify the presentation of this supplementary note.

I am greatly indebted to Wilhelm Bock for his generous permission to describe the new specimen and for his hospitality during my stay in Philadelphia, as well as for his judgement on several controversial points. Without his cooperation in furnishing materials and photographs for study, this paper could not have been written. Hearty thanks are also due to Professor James L. Dyson of the Department of Geology, Lafayette College, for the loan of the type specimen; and to Drs. Joseph T. Gregory at Yale and Albert E. Wood at Amherst for their hospitality in facilitating my study of footprint specimens there. Dr. John C. Harper of the Department of Geology, University of Liverpool, has been most generous in furnishing data and literature on Keuper footprints in the Liverpool museums. Photographs for the plates were supplied by the Academy of Natural Sciences of Philadelphia through the courtesy of Dr. Horace G. Richards. My indebtedness to Professor Richard S. Lull for pleasant and stimulating discussions is gratefully acknowledged.

SOURCE OF THE MATERIAL

Obviously the type locality cannot be both Milford, New Jersey, and Sanatoga, Pennsylvania. It is suggestive to note that another specimen from the same private collection as the *C. lulli* trackway slab, the type of *Chirotherium copei* Bock, was labeled as having come from a quarry near Washington's Crossing on the Delaware River although internal evidence demonstrates beyond doubt that it actually came from the gray sandstone layer of the Smith Clark quarry at Milford. With this example of mislabeling in mind we may justifiably discount the Sanatoga label.

Although the source of the Lafayette College type cannot be proved, it is part of a collection made by John Eyerman, whose only recorded collecting of fossil footprints was done at the Milford quarries in 1885 and 1887. No reference is made to this specimen in the early reports on the Lafayette collection, but (as I will point out in a subsequent

paper) grave ambiguities exist in both accounts. Bock (1952, p. 416) reports that a bed of red-brown shale bearing water-flow marks like those on the footprint slabs crops out in the Smith Clark quarry some 15 meters above the gray sandstone horizon which bears the *Chirotherium parvum* faunule. Thus it appears fairly probable that, as stated in the original description, the single known individual of *Chirotherium lulli* was found in the Smith Clark quarry near Milford, Hunterdon County, New Jersey. The type horizon (as determined by Bock) lies in the upper Brunswick formation some 5,100 meters above the base of the Newark series, Upper Triassic.

REDESCRIPTION OF THE SPECIES

Order THECODONTIA

Suborder PSEUDOSUCHIA

Family CHIROTHERIIDAE Abel, 1935

Genus CHIROTHERIUM Kaup, 1835

LARGE-MANUS GROUP of Peabody, 1948

CHIROTHERIUM LULLI Bock

Bock, Wilhelm, 1952. Jour. Paleontology, 26, p. 415, pl. 49, fig. 7.

Type. Lafayette College Geological Museum S491, a left manus-pes set (inadvertently cited as right in the original description). Academy of Natural Sciences of Philadelphia, Wilhelm Bock collection, four consecutive manus-pes sets in relief, the third of which is the counterpart of S491. As these specimens represent the same individual, both constitute the type in the sense of Simpson (1940); for the type of a zoological species is (at least in non-colonial forms) most reasonably regarded as an individual animal, the sum of all its parts however many museum specimens these may comprise.

Diagnosis. A diminutive species of the large-manus group. Trackway relatively wide with pace angulation of 150° ; manus apparently elongate and prehensile; pes broad and strongly toed-out, characterized by oblique cross-axis, relatively long and subequal digits II and IV, and functionally posterior digit V with well-developed metatarsophalangeal pad. Measurements in Tables 1 and 2.

TABLE 1
COMPARATIVE MEASUREMENTS OF SMALL, LARGE-MANUS
CHIROTHERIID

Data on the three Lower Triassic (Moenkopi) species from Peabody, 1948.				
	<i>C. lulli</i>	<i>C. diabloensis</i>	<i>C. cameronensis</i>	<i>C. minus</i>
Stride, mm.	232	270	425	750
Pes length, mm.	44	53	50	85
Stride : pes length	5.3:1	5:1	8.5:1	9:1
Pace angulation	150°	140°	161°	164°
Pes divarication	29°	22°	13°	12°
Manus divarication	same	same	none	none
Angle, cross axis to digit III axis	ca. 68°	55°	55°	70°

Trackway. As body bulk has a definite effect on trackway pattern, the well-known smaller species of *Chirotherium* serve best for comparison with the diminutive *C. lulli* (see Table 1). From its proportions the type trackway appears to have been made by a walking rather than a running individual. The pace angulation and the ratio of stride to pes length are unexpectedly low for an Upper Triassic species, in which cursorial specializations might be expected; indeed these characters compare most closely with those of the primitive Lower Moenkopi species *C. diabloensis*. Perhaps these trackway proportions are as much a function of size as they are criteria of primitive organization.

The pes is toed-out to an unusual degree, the axis of digit III forming an average angle of 29° with the trackway midline. (The functional significance of this arrangement is discussed below.) Pes and manus are turned out at about the same angle. This is just the relationship found in *C. diabloensis* and contrasts with the situation in *C. cameronensis* and *C. minus*, in which the pes divarication is only about half that of *C. lulli* and the manus points directly forward. Large chirotheriids, however, in general have the manus turned out as far as the pes or (in *C. barthii*) even farther.

On the assumption that the animal's gait was alternating, i.e. that the left manus and right pes were implanted at essentially the same time, the gleno-acetabular length of the trackmaking reptile may be determined by the method used with primitive tetrapods (Baird, 1952, p. 834). This method is detailed below in the section on skeletal restoration. The agreement of figures, 142 and 145 mm., obtained

from measurements over two segments of trackway is well within the limits of probable error. The slight overlap of the right pes onto the adjacent manus print might indicate that the manus print had previously been vacated, hence that the gait was not strictly alternating; but an overlap of this size could well occur with the manus still partially implanted but in the roll-off phase.

Manus. As may be seen from Plate 1, the left manus imprint lies nearly a centimeter ahead of the pes, with the axes of the third digits nearly in alignment. Though digits IV and V impressed only faintly, digits I-III recorded their full lengths. The right manus imprint, in contrast, lies just medial to the pes with its postero-lateral border slightly overlapped by the tip of pes digit II. Here digit impressions are wholly lacking and the imprint is ovoid, apparently representing the metacarpo-phalangeal pads and part of the adjacent sole. Whether this anomaly is caused by a malformed right manus or merely a normal variability in gait cannot be determined from this short trackway of a single individual.

For the details of manual anatomy we must rely almost entirely on the third manus-pes set which is fortunately preserved in counterpart. The imprint is incomplete, lacking digit V and much of IV, and is none too clear in the details recorded. Undue faith should not, therefore, be placed in the observations which follow.

The table of measurements compiled by Boek can now be supplemented on the evidence of the counterpart trackway (see Table 2).

TABLE 2
MEASUREMENTS OF *CHIROTHERIUM LULLI*, TYPE

Digit lengths include metacarpo- or metatarso-phalangeal pads;
pes digit V measured along curved axis.

	MANUS	PES
Area, mm. ²	est. 180	360
Length, mm.	22	44
Width	est. 20	26
Length, I-IV group	19	30
Width, I-IV group	16	23
Length, digit I	8	17
II	15	22
III	19	27
IV	? 15	24
V	?	18
Pace (average of 3)		117

As restored the manus has a surface area approximately half that of the pes. This ratio is high even for a member of the large-manus group, in which the manus area is more typically one-third to one-quarter that of the pes.

The manus is characterized by moderately divergent, elongate digits with distinct articular pads which indicate a phalangeal formula of 2-3-4-?-?. Peabody (1948, p. 401) has derived the same formula from rare specimens of *C. diabloensis* and deduces that the complete formula was probably 2-3-4-5(4?)-3. Digit I is offset laterally and set well back, suggesting that metacarpal I was unusually short. The proximal phalanges of digits II-IV seem to be united into a solid palm, so that the interdigital salients penetrate only to the level of the joint between phalanges 1 and 2. Digits II and III appear to be clawed; only the base of IV is preserved. Very little can be said about the fifth digit, as impressions which might be attributed to it bear different relationships to successive impressions of the left manus. (Considerable variation in the divarication of digit V in single trackways of *C. minus* has been noted by Peabody, 1948, p. 362). The position shown in Figures 1 and 2 is that indicated by the third manus-pes set, but the evidence is weak indeed.

No species of *Chirotherium* known to me has a less specialized manus than this; a closely comparable organ is found only in *C. cameronensis* from the Upper Moenkopi. The long, clawed digits with their individually padded joints indicate the retention of a grasping function which had been lost by all other chirotheriids except perhaps the small, primitive Lower Triassic species *C. diabloensis*, *C. cameronensis*, and *C. minus*, the Upper Triassic *Synaptichnium* (see Figure 1 B-E), and an unnamed Bunter species from southern France (Charles, 1949). Such a long-fingered, grasping manus is unique among Upper Triassic species of *Chirotherium*, for even in early Moenkopi (early Bunter) time the typical chirotherian manus had already become rather compact and inflexible, and a hoof-like manus characterizes all the other known Keuper species.

Pes. An optimum of information on pedal structure is revealed by the remarkably clear detail of the second pes imprint (Plate 2, figure 1), verified by the evidence of the other three. Digits I-IV form a relatively broad group, the posterior margin of which is not clearly defined, separated from digit V by a relatively wide sulcus. Metatarsophalangeal pads I-IV are faintly separated by very shallow sulci; the curvature of the broad arc in which they lie is of course due both

to transverse arching of the distal end of the metatarsal bundle and to differences in metatarsal length. The cross axis (drawn between pads I and IV) intersects the long axis of digit III at an angle which is less acute than in the primitive species *C. diabloensis* and *C. cameronensis* (see Table 1) but more acute than in most other species, in which the angle approaches 90°.

The first four digits are sub-parallel with a total divarication of less than 20°; they are separate rather than basally appressed, so that wide interdigital salients extend back almost to the level of the metatarso-phalangeal joints. All bear long sharp claws. Articular swellings, which are visible both in outline and as rounded, confluent elevations on the ventral surface, indicate a normal reptilian phalangeal formula. The digits as a group are rather short in relation to the width of the metatarsal bundle; IV is slightly shorter than III, and II is nearly as long as IV. This pattern of relative digit length

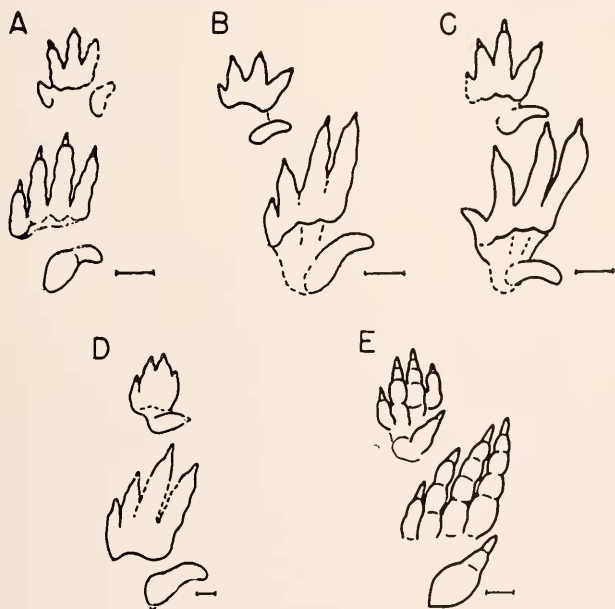


Fig. 1. Small chirotheriids of the large-manus group, similarly oriented for comparison. **A.** *Chirotherium lulli*; **B.** *C. diabloensis*; **C.** *C. cameronensis*; **D.** *C. minus*; **E.** *Synaptichnium pseudosuchoides*. **A-C** $\times 1\frac{1}{2}$, **D** $\times 1\frac{1}{4}$, **E** $\times 3$ s. **B, C, D** from Peabody, **E** from Smith Woodward.

differs from that of other small chirotheriids (see Figure 1) but compares more closely with that of the large species *C. barthii*.

Digit V, unlike that of the other small species, bears a well-developed metatarso-phalangeal pad which impressed at every step. The digit as a whole is set rather medially so that the presumed position of its metatarso-phalangeal joint is in line with the long axis of digit IV; thus the phalangeal part, though of average proportions, projects laterally somewhat less than it does in the other small species. This phalangeal segment is clearly demarcated from the pad and shows (in the second imprint) faint constrictions and nodes which indicate the presence of three phalanges; the minute rudiment of a fourth may or may not have been present.

Here we have a foot in which the first four digits could apparently be flexed independently on the metatarsals like human fingers, and must have retained the primitive grasping ability which had been sacrificed in most chirotheres to cursorial specializations. The thumb-like fifth digit, which primitively served to prop the chirotherian foot at right angles to the direction of movement, is fully developed and — when seen in the isolated footprint — appears to have lost little of this function. But this appearance is totally misleading, as the new-found trackway reveals. On the contrary, the foot in walking is toed-out so strongly that the entire length of digit V falls behind the pads of the first four metatarsals and medial to most of the free length of digit IV: the lateral propping function of the “thumb” has been entirely lost.

A striking parallel to this development is found in a British Middle Keuper chirotheriid designated as “form L” by Beasley (1904, p. 229, pl. 7) and named *Chirotherium beasleyi* by Nopcea (1923, p. 144).¹ A trackway from Storeton, Cheshire (British Museum [Natural History] R.729) shows this to be a long-striding form rather similar in size and shape to *C. minus* (see Figure 1 D), though pes digit I is slender and almost non-functional and digits II–IV form a strong, symmetrical group. The pes is toed-out to about the same extent as in *C. lulli*, and digit V is (as Beasley observes) set well back and close to the middle line of the foot. Such a structure could readily have developed from that of the presumably ancestral *C. minus* by a medial shift of the distal end of metatarsal V.

Similar features are shown by another British Keuper form designated as footprints of *Rhynchosaurus* by Smith Woodward (1902).

¹ *Non C. beasleyi* Peabody, 1948; the latter species is renamed in an appended note, page 189.

as form "D 3" by Beasley (1905, p. 277), and as *Synaptichnium pseudosuchoides* by Nopcsa (1923, p. 142; see also Abel, 1935, fig. 50). This species (Figure 1 E) is somewhat younger than the last and comes from Chillington, South Staffordshire. In form it is (as Nopcsa concludes) more pseudosuchoid than rhynchosauroid, with the pes impressing behind the manus rather than beside or ahead of it. The whole aspect suggests a long-fingered small chirotheriid of the large-manus group, the chief difference lying in the straightness and sharp claws of manus and pes digits V.² In both manus and pes the fifth digit is set medially and entirely behind the other four; the pes is more toed-out than the manus but its exact divarication from the trackway midline is unknown.

In these two English species as in *Chirotherium lulli*, pes digit V can have acted only as a posterior, not a lateral prop. This fact in itself is no distinction, for partial or complete loss of the fifth digit's lateral propping function is so common among Keuper chirotheriids of both large-manus and small-manus groups as to be almost characteristic of the period. But the methods by which this modification of function was accomplished are varied. An examination of this variety in method offers us some insight into problems of pedal adaptation among late Triassic pseudosuchians as well as useful criteria for differentiating the various footprint species.

At least five processes are involved, either singly or in combination: *shortening* or virtual elimination of the phalangeal segment of digit V, *attenuation* of this segment, *straightening* it to reduce the lateral projection, *medial shift* of the distal end of metatarsal V and thus of the metatarso-phalangeal pad, and *toeing-out* to rotate digit V to the rear. The incidence of these processes in some of the better-known Keuper chirotheriids may be tabulated as follows. Parentheses indicate a slight modification; a dash, that the trackway is unknown.

Chirotherium lulli is unusual in having achieved such a modification without losing the primitive grasping ability of the foot. This ambivalence of pedal adaptation may well have been one of the factors which enabled *C. lulli* to survive all its relatives.

² Discussion of the relationships of this remarkable form to *Chirotherium* and to such quasi-chirotherioid species as *C. angustum* Huene and *Thecodontichnus verrucosus* (Tommasi) from the Verrucano of Italy, and *Gwyneddichnium minore* Bock from the Lockatong of Pennsylvania, is unfortunately beyond the scope of this paper.

	Shortening	Attenu- ation	Straightening	Medial shift	Tearing-out
LARGE-MANUS:					
<i>C. lulli</i> Bock				x	x
<i>C. beasleyi</i> Nopesa				x	x
<i>Synaptichnium pseudo-</i> <i>suchoides</i> Nopesa		x	x		?x
<i>C. angustum</i> Huene	(x)			x	—
<i>C. wondrai</i> Heller		x	x	x	—
SMALL-MANUS:					
<i>C. lomasi</i> nom. nov.	(x)				x
<i>C. parvum</i> (Hitchcock)	x				—
GROUP UNCERTAIN:					
<i>C. herculis</i> Egerton					
(?= <i>C. bipedale</i> Abel)	x			x	
<i>C. thuringiacum</i> Rühle	x				—
<i>Brachychirotherium</i> <i>hassfurtense</i> Beurlen	x		x		—
Eyerman's <i>chirotherium</i> (Beird MS)	x				—

RELATIONSHIPS

Because of the equivocal nature of the footprint record it is necessary to examine the relationships of *Chirotherium lulli* as a member both of the form-family Chirotheriidae and of some family of the Pseudosuchia.³ Comparison with skeletal remains may however be deferred for consideration in connection with an attempted reconstruction of the pedal skeleton.

³ Abel (1935, p. 67) proposed the Chirotheriidae as a family of the order Pseudosuchia, diagnosed both by footprint characters and by inferred skeletal structure. This treatment is however unworkable because of eventual overlap with some osteologically-based family of reptiles (if not several) — an overlap which cannot be resolved by the rule of priority because footprints and skeletons can almost never be correlated to the point of synonymy. A more realistic and practical procedure is to treat the Chirotheriidae as a form-family of footprints, diagnosed on observed characters only, and correlative with some part of the zoological order Pseudosuchia although taxonomically distinct. Such a procedure has ample precedent in the long-established use of form- and organ-categories in paleobotany and invertebrate paleontology. It preserves the proven advantages of the Linnaean system of nomenclature as contrasted with systems of formula-names or para-Linnaean categories.

Chirotherium lulli shows a curious assemblage of presumably primitive and specialized characters which are segregated in the tabulation below:

PRIMITIVE	ADVANCED
GENERAL	
Wide trackway (low pace angulation).	Pes V functional as posterior, not lateral prop.
Low stride-to-pes length ratio.	
Prehensile manus and pes.	
MANUS	
Elongate, clawed digits.	Metacarpal I apparently short.
PES	
Oblique cross axis.	Group I-IV broad.
Fairly long digit V widely separated from I-IV.	Long II; IV shorter than III but longer than II.
	Distinct metatarso-phalangeal pad on medially set V.

Comparisons with Lower Triassic chirotheriids of the large-manus group may be summarized by the statement that most of the characters listed fall within the range of specialization of species from the American Moenkopi and the European Bunter. *Chirotherium lulli* is readily distinguished from all of these, yet in morphology it is close to them; and were it not for the facts of stratigraphy and the associated tracks of dinosaurs, it might reasonably be assigned to the Lower Triassic. High in the Upper Triassic it is in many ways anachronistic.

The comparisons with European Keuper chirotheriids which were made in the preceding section indicate that while *Chirotherium lulli* resembles many of them in single characters or adaptive groups of characters it shows no close relationship to any. The other Upper Triassic chirotheriids from North America likewise offer few points of comparison. All the known specimens were found by the same collector in the same quarry near Milford, New Jersey, in a gray sandstone-over-shale sequence of the Brunswick formation some 15 meters below the horizon of *C. lulli*. Two basic structural types are present. The first, including *C. parvum* (C. H. Hitchcock) and *C. copei* Bock, represents a highly specialized lineage of the small-manus group and so does not concern us here. The second is an undescribed species known from a single deep pes imprint collected for the Museum of Comparative Zoology by John Eyerman in 1887. Preliminary exami-

nation indicates that this is a large-manus species of average size and not too different from *C. lulli* in general proportions. But in the structure of the fifth pes digit they are as unlike as possible, for *C. lulli* has a differentiated phalangeal segment of normal length while Eyerman's chirotherium has nothing but a compact, scale-bordered metatarso-phalangeal pad — the ultimate in digit reduction among Chirotheria.

Chirotherium lulli thus appears (on the evidence now available) to represent an independent lineage of the large-manus group which, though it paralleled other Keuper species in several respects, retained many characters more typical of Bunter species. Though probably not derived from any small, primitive Bunter form now known, it may have had ancestors in common with one or more of them.

SKELETAL RESTORATION

The skeletal restoration offered in Figure 2A is based on the assumption, supported by comparison with living reptiles and cursorial birds, that the toe joints correspond to the nodes and pads of the footprints. Except for manus digits IV and V, the form of which is conjectural, the basic skeletal pattern was restored entirely on the evidence of the footprints themselves and without reference to the pedal osteology of any fossil reptile. The result nevertheless conforms to the structure of known Triassic reptiles of the suborder Pseudosuchia, to which the Chirotheriidae have been referred for reasons succinctly stated by Peabody (1948, p. 395).

To find an approximate skeletal parallel for the pes of *Chirotherium lulli* we need look no farther than *Euparkeria*, a Lower Triassic genus of the family Ornithosuchidae. As may be seen in Figure 2B the pes of *Euparkeria* closely resembles the restored skeleton of *C. lulli* and is almost exactly the same size. Significant differences are, however, evident: in *Euparkeria* the metatarsal bundle is narrower and metatarsal I is decidedly shorter, so that the footprint of this genus is (as Peabody has pointed out) rather to be sought among the small Bunter chirotheriids with very oblique cross axes. A more striking difference lies in the position of the fifth metatarsal, the distal end of which in *C. lulli* must have lain directly beneath the shaft of the fourth: — the "thumb" was, if not appposable, somewhat apposed. Some experimentation with an enlarged model convinces me that the pes of *Euparkeria* cannot be made to conform to this pattern without doing

violence to the articulation between metatarsal V and the calcaneum and tarsale. Here again the closest parallel to *Euparkeria* is to be

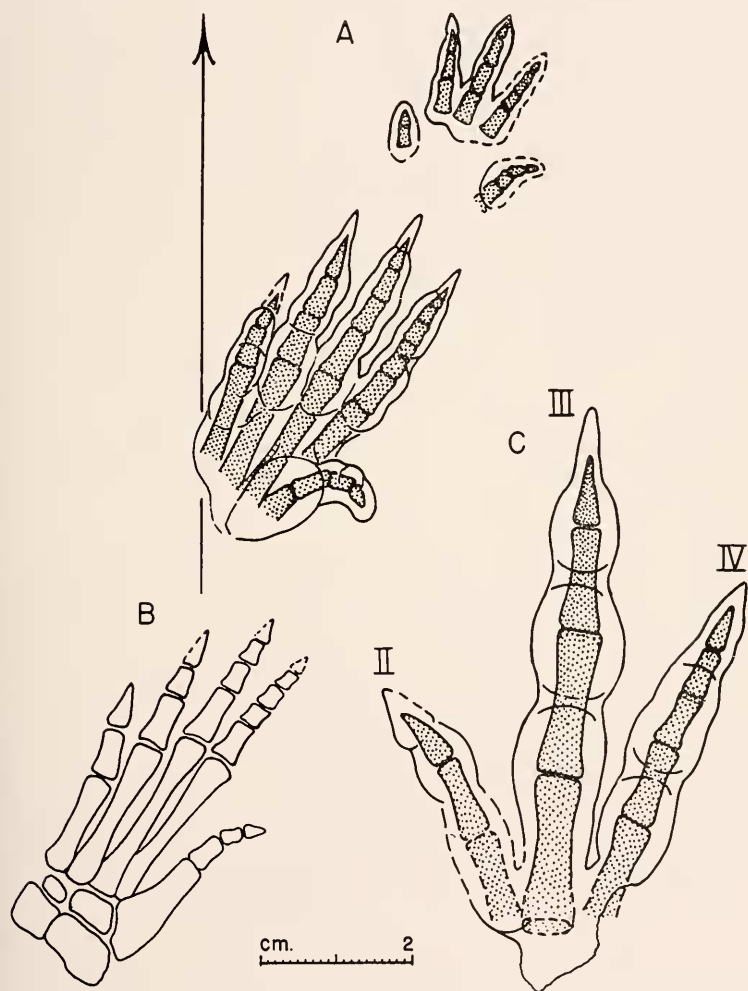


Fig. 2. **A.** *Chirotherium lulli* Bock, composite outline of right manus and pes with skeleton restored, x 1. Arrow represents midline of trackway. **B.** Pes of *Euparkeria capensis* Broom, x 1, modified from Broom after Schaeffer. **C.** Right pes imprint of the associated dinosaur, with phalanges restored, x 1.

found in a small Bunter chirotheriid such as *C. minus* (Figure 1D) in which the fifth metatarso-phalangeal pad is offset laterally.

The few Upper Triassic ornithosuchids whose feet are known are, like *Euparkeria*, only approximately comparable. *Saltoposuchus* may be eliminated as too far advanced in bipedality; the quadrupedal reconstructions by von Huene (1921, figs. 31, 32), in which the femora are essentially horizontal, cannot be manipulated to produce a chirotherioid trackway. The pes of *Ornithosuchus* (see Colbert, 1952, fig. 32B) differs significantly from the restored pes of *C. lulli*: digit I is the most robust and has a very short metatarsal, while metatarsal V is long and slender, lacking the proximal hook of *Euparkeria*, and bears a slender digit with elongate phalanges.

The pes of *Hesperosuchus* from the Chinle of Arizona, which has been restored after that of *Ornithosuchus* by Colbert (1952, fig. 31), is too incomplete for valid comparison with the restored skeleton of *C. lulli*. Its much larger size and proportionately longer phalanges appear to preclude any correlation. Although the manus is relatively large there is still no evidence to justify correlation of *Hesperosuchus* with the large-manus group of chirotheriids or (for that matter) with *Chirotherium* at all.

One Upper Triassic ornithosuchid in which the first four metatarsals correspond in relative length with those restored for *C. lulli* is *Pedeticosaurus* van Hoepen (1915, pl. 13) from the Karroo. Here no fifth digit or metatarsal is preserved, so comparison with *Chirotherium* is impossible.

Obviously there is insufficient material of both feet and footprints to permit valid or even tentative correlation between particular chirotheriid species and pseudosuchian genera. Nevertheless the body proportions of the reptile which produced the *Chirotherium lulli* footprints can be determined from the trackway and compared, in a general way, with those of ornithosuchids.

In computing the gleno-acetabular length of the trackmaker from the *Chirotherium lulli* trackway I assume that the gait was alternating as in living Archosauria, with the forelimb and hindlimb of opposite sides operating more or less simultaneously. Thus at one moment in each cycle of progression all four feet were in contact with the ground in such a manner that the left feet occupied a manus-pes set of footprints while the right pes was still implanted in the preceding set and the right manus had just impressed the first footprint of the next set. This situation is represented in Figure 3; a comparable stage in a



Fig. 3. A trackway of *Chirotherium lulli* Bock being made by an ornithosuchid pseudosuchian (restoration based on *Ornithosuchus* and *Euparkeria*).

walking sequence of *Alligator mississippiensis* is shown by Schaeffer (1941, fig. 17B) in a drawing made by projection from a motion picture.

At this moment in the cycle the center of the acetabular axis lies about midway between the tarsi, and that of the glenoid axis lies about midway between the carpi. To determine gleno-acetabular length from a trackway, therefore, we need only locate the midpoints between the carpal and tarsal areas, respectively, of four simultaneously-occupied footprints. The distance between these midpoints will represent a close approximation to the actual gleno-acetabular length of the trackmaker.

Quite a different method, it should be noted, has been used by Soergel (1925, p. 57) to determine the gleno-acetabular length of *Chirotherium*. The basic assumption of this method is that the movements of the opposite forelimb and hindlimb were one-half out of phase, so that at a moment when the center of the acetabular axis was midway between the implanted pedes, the glenoid fossa was directly above an implanted manus. Thus in his figure 51, where the left pes is in advance of the right, Soergel measures the "Rumpflänge" from the midpoint between the pedes to the next right manus imprint. The resulting measurement is exactly a quarter-stride longer than that obtained from the same trackway by my method.

We have observed that forelimb and hindlimb movement are essentially in phase in the Crocodilia, the closest living relatives of the Chirotheria. The wide straddle of *Alligator mississippiensis* and the nearly linear trackway of *Chirotherium barthii* are merely variants on the basic tetrapod trackway pattern, the differences between them being largely compromised in the trackway of *Chirotherium lulli*. Thus argument from analogy, though not conclusive, supports the interpretation offered here.

An out-of-phase pattern of limb movement such as that postulated by Soergel is characteristic not of reptiles but of mammals, whose physiology permits the development of gaits specialized for speed. Even the speed-adapted mammals, nevertheless, tend to revert to an alternating gait for leisurely progress. Whatever the appearance of the galloping, running, loping, pacing, or leaping trackways of such animals, the walking trackways in general consist of alternating left and right manus-pes sets. (Overlap or super-position of pes and manus imprints may obscure the basic pattern of sets. See Jaeger, 1948.) Although the mammal's opposite fore and hind feet may not move

exactly synchronously at a walk, they are essentially in phase, and a reasonably close approximation of the animal's gleno-acetabular length may be determined from the trackway. Thus even if *Chirotherium* were capable of a rapid, out-of-phase gait, this would probably not be the gait at which it made a trackway of alternating manus-pes sets.

Having determined the basic body measurements of *Chirotherium lulli* we can now attempt to restore the trackmaker on the basis of an ornithosuchid of appropriate size and proportions. Dearth of skeletal material hinders the attempt, but by using *Ornithosuchus* as a model and modifying its proportions slightly after those of the more closely comparable but incompletely known *Euparkeria*, we may arrive at a fairly convincing restoration.

In the preparation of Figure 3 von Huene's reconstruction of *Ornithosuchus* (from Gregory, 1951, fig. 14.2) was enlarged until its gleno-acetabular length equalled that of *C. lulli*, and its feet were aligned with four simultaneously-occupied footprints of the trackway. The length of the fore limbs determined the shoulder height. As only the distal ends of the metatarsals impressed, the metatarsus had to be raised; the pelvis was also raised to give the femur the nearly vertical antero-posterior swing which is indicated both by its construction and by the narrowness of the trackway. The resulting figure is believed to represent with reasonable fidelity a small ornithosuchid in normal quadrupedal walking pose; it is also decidedly similar (with the exception noted) to the restoration of *Chirotherium barthii* which Soergel (1925, figs. 53, 54) derived from the trackways alone.

THE ASSOCIATED DINOSAURS

Slightly overlapping the fourth pes imprint of *Chirotherium lulli* (Plate 1 and Plate 2, figure 3) is the left pes imprint (reversed in the photograph) of a small tridactyl dinosaur. Most of the details are clear enough that a fairly reliable reconstruction of the form can be made from this single imprint. The slender digits bear triangular claws and well-defined articular nodes from which a normal theropod pedal skeleton may be reconstructed (Figure 2C).⁴

Digit II is shorter and more divergent than IV; both are placed well forward so that the joints between their first and second phalanges

⁴ My figure shows joints consistently reconstructed opposite nodes; in this respect it differs fundamentally from the reconstructions of Lull (1915) and slightly from those of Heilmann (1927, fig. 130 K) and Peabody (1948, fig. 37). A detailed critique of these various interpretations is included in my forthcoming study of the other reptile footprint faunules from Milford.

lie opposite the distal part of the first phalanx in digit III. If the lateral digits were rotated parallel, the tip of claw II would lie opposite the distal end of phalanx 2 in digit III; that of claw IV, the distal end of phalanx 3. The digits diverge almost from a common base: their long axes intersect just posterior to the metatarso-phalangeal pad of digit III.

Characteristic though it is, this type of foot is difficult to match among the well-known footprint genera of the Upper Triassic. The slender digits and pointed claws suggest the small, tridactyl coelurosaurs whose footprints comprise the family Grallatoridae, but the species of *Grallator* proper (one of which occurs in another Milford faunule) have lateral digits set well back on the foot with their claw-tips nearly opposite, claw II being slightly in advance. The Manchuurian grallatorid *Jeholosauripus* (Shikama, 1942, fig. 1) more closely resembles the Milford form in position and divarication of digits but is proportionately shorter, with a relatively longer digit II and shorter IV.

Coelurosaurichnus toscanus Huene (1941, p. 14) from the Verrucano of Italy is more closely comparable to the Milford footprint in size and proportions, particularly in the length of digit IV. In the type imprint the base of the foot appears to be shod with a large, roughly circular "Metatarsalpolster," but this may be an artefact of impression: in another footprint of the same species (Fueini, 1936, pl. 76 near top) the lateral toes are less divergent and seem to have individual, oval metatarso-phalangeal pads of grallatorid form. Unfortunately, the genus *Coelurosaurichnus* is founded on inadequate material and has been loosely construed by subsequent authors to include any Keuper footprints of coelurosauroid type.

The Connecticut Valley pes imprints which are most similar in digit proportions and arrangement pertain to *Tarsodactylus caudatus* E. Hitchcock. This form, unlike the grallatorids cited above, is a quadruped with a broad trackway and a pentadactyl manus which is strongly toed-out and impressed lateral to and usually in advance of the pes. The Milford track may be interpreted as a *Tarsodactylus* whose manus imprint lay just beyond the broken edge of the slab; but in this case the next manus-pes set should appear on the surface. Another Massachusetts form in which digit IV is longer than II is *Anomoepus scambus* E. Hitchcock; but here disparity in digit length is much less marked than in the Milford imprint.

Closest comparisons are to be made with certain nameless foot-

prints from beds of approximately equivalent age in south-central Pennsylvania. The cast of an imperfectly recorded pes imprint which is nearly identical in size and structure with the Milford track is preserved at Yale (YPM 3765). This specimen was collected at Hess' or Wentz's mill on Big Spring Run about 1 mile ENE of Yocumtown, New Cumberland quadrangle, York County, Pa., and is labeled as having come from the upper part of the Conewago formation (New Oxford of Stose). According to Stose and Jonas' (1939) map of York County, however, this locality lies not in the New Oxford but in the overlying Gettysburg shale. The label notes, "stride about 18 inches," but this cannot be verified.

Another footprint of this type, from an unspecified locality near Yocumtown, has been figured by Hickock and Willard (1933, fig. 6B). This track is interpreted as a left pes. The presence of three well-defined articular nodes in digit "II," however, is evidence that at least three phalanges impressed their full lengths. If the first articular node (like that of digit III) marks the joint of phalanx 2 with a proximal phalanx which sloped upward to its metatarsal, then at least four and probably five phalanges were present in digit "II": it must therefore be IV, and the foot a right pes.

In this imprint digits II and IV are shorter and digit II less divergent than in the Milford and Yale tracks, though it is similar in the other details recorded. The length and anterior position of digit IV debar this specimen from the species to which Hickock and Willard assigned it, *Anchisauripus sillimani*. Without examining the material I cannot agree or disagree with their generic assignment.

Although no name can at present be assigned to the New Jersey footprint, a better understanding of its affinities would seem to depend on a comprehensive study of dinosaur tracks from the Keuper of Pennsylvania.

On the back of the *Chirotherium lulli* slab, separated from the other tracks by a few millimeters of sediment, is a second small tridaetyl footprint of quite another sort (Plate 2, figure 2). This track is even less determinable than the first, but because it is essentially a member of the same faunule let us dutifully but briefly examine its affinities. The foot, a left pes, is thick-toed and relatively broad. The slightly divergent lateral digits are set back from the base of a rather short digit III; IV extends a little beyond the tip of II and shows a faint metatarso-phalangeal pad.

This sort of foot is found in the Newarkian genera *Eubrontes*,

Anchisauripus, and *Sauropus*. Gigantic *Eubrontes*, the smallest species of which is more than three times as large, can be omitted from consideration. Worthwhile comparisons narrow themselves to two species: *Anchisauripus guymeddensis* Bock (1952, p. 406) from the Lockatong formation of Pennsylvania, and *Sauropus barrattii* (E. Hitchcock) from the Portland arkose of Massachusetts (Lull, 1915, p. 217). *A. guymeddensis*, known from a single indistinct imprint, is very similar though half again as large and a little narrower in proportion. Equally poor preservation increases the similarity. One feature of both which may be significant is the concave medial margin of digit II, a feature which is more typical of the semi-biped *Sauropus* than of *Anchisauripus*. My conclusion from this meager evidence is that the second dinosaurian footprint probably belongs to the same genus as *A. guymeddensis*, though whether that genus is really *Anchisauripus* remains to be seen.

Nearly all the forms cited require further study before their interrelationships can be determined. One potent source of confusion, I suspect, is that the Keuper "dinosaur" footprints were made not only by Saurischia and Ornithischia but by advanced bipedal Pseudosuchia as well. Cases of homeomorphism in foot structure among members of the three groups are to be expected, and the detection of such cases on the evidence of footprints alone will be nearly impossible.

The discerning reader has, I hope, winnowed one kernel of truth from the foregoing discussion: that a single imprint, in which individual anomalies of form and peculiarities of impression may be concealed, has no taxonomic value within so homogeneous a group as that of the ornithoid "dinosaur" footprints. This otherwise nearly profitless survey can at least serve to emphasize — it could hardly overemphasize — that ornithoid footprints cannot be diagnosed and classified without adequate quantities of well-preserved material, preferably trackways. To base new genera and species on isolated, poorly preserved footprints is useless; to base stratigraphic correlations on them is usually misleading.

SIGNIFICANCE OF THE FAUNULE

This reptile faunule, though it consists only of three essentially contemporaneous individuals which have a known geographic range of two square feet, presents some interesting problems in chronology and ecology. Associations of Keuper chirotheriids with dinosaurs in

England and on the Continent have been known for more than a century. (Heller, 1952, presents a useful tabulation of twentieth-century central European finds.) Such an association in this country was reported by C. H. Hitchcock in 1889 but not demonstrated until Bock's 1952 restudy of the New Jersey footprints; and the occurrence announced in this paper is only the second on record.⁵

Now this is very strange. Ornithoid dinosaurian trackways were found in the Upper Triassic of the Connecticut River valley as early as 1802, and in the subsequent century-and-a-half a rich series of faunas has been assembled from more than forty localities in Massachusetts and Connecticut. While footprints are not known from the New Haven arkose,⁶ the lowest formation of the Connecticut Valley Newarkian sequence, they are abundantly represented in the overlying Meriden formation (the anterior and posterior shales and sandstones of earlier authors) and the upper series of sandstones and shales now known as the Portland arkose (Krynine, 1950). Specimens in museums must number at least 40,000.

Associated with the dinosaur footprints are several varieties of trackway, typically quadrupedal, resembling *Chirotherium* except for the absence of a functional fifth pes digit. *Batrachopus* is representative of this group. Most of these forms are small, having pes lengths ranging from 15 to 75 mm., and are logically correlated with the smaller varieties of *Pseudosuchia*. The single exception, *Otozoum*, is so large (490 mm.) that although its foot is merely a graviportal, bipedal modification of the *Batrachopus* type its affinities have previously been sought among dinosaurs rather than pseudosuchians.

But among these numerous and varied trackways of pseudosuchioid form no *Chirotherium* has ever been found. Although nothing can be said about New Haven time, the available evidence for the absence of chirotheriids from the Connecticut Valley basin in Meriden and Portland time is exceedingly weighty. On the other hand, the New Jersey-Pennsylvania basin, whose footprint faunas have been much less intensively collected and studied, has yielded eight specimens representing three clearly defined species of *Chirotherium*. If the *Chirotherium*-bearing Brunswick formation of New Jersey is a time equivalent of the Portland arkose, as Bock (1952, p. 430) has implied,

⁵ An association of possibly chirotherioid with possibly dinosaurian tracks from Virginia was described by Shaler and Woodworth in 1899. The second and fourth footprints in their rather diagrammatic figure 90 have a vague resemblance to *C. lulli* and its companion dinosaur, but the evidence is inconclusive.

⁶ A New Haven find, unfortunately never collected, is mentioned by Lull, 1915, p. 94.

then some barrier — topographic, climatic, or biotic — must have prevented the spread of chirotheriids into the Connecticut Valley basin while it permitted the intermigration of small bipedal dinosaurs.

Such a barrier can hardly have been an upland, a permanent desert, or an impassable river. According to Krynine (1950, pp. 195–196):

“Central and western Connecticut during Newark time can be pictured as a wide flatland, bordered on the east by the steep but relatively low hills of the Great Fault scarp and to the west merging insensibly into the somewhat similar flatland of southern New York and New Jersey. The interfluvium between these two basins may have been so low as to lack any topographic expression, but it probably still was a divide between the two sedimentation basins of Connecticut and New Jersey. A master stream meandered over this flatland, probably flowing southward . . .

“The climate was hot and seasonally very humid. During the wet season heavy, long-continued rains transformed the flatland into a vast, sticky, water-soaked morass . . . During the dry season a broiling sun was beating upon the Connecticut savanna, caking and cracking the red soils. However, dense and luxuriant forests extended for several hundred yards on each side of the numerous watercourses, providing food and a cool shelter for the reptilian denizens of the Newark.”

The cosmopolitan flora of the Triassic precludes any stringent climatic zonation. A biotic barrier which would affect cursorial, carnivorous pseudosuchians but not cursorial, carnivorous dinosaurs is of course possible but is very difficult to conceive.

Additional arguments for the distinctness of the Brunswick reptile faunas from those of the Meriden and Portland must await the description of new footprint types from the *Chirotherium parvum* horizon at Milford, now in manuscript. Nevertheless, it is not premature to state that the evidence of two *Chirotherium* faunas strongly suggests that the footprint-bearing sequence of the upper Brunswick formation which is exposed in the Smith Clark quarry at Milford, New Jersey, antedates not only the Portland arkose but the underlying Meriden formation as well, and more probably correlates with the New Haven arkose.

This conclusion is compatible with the tentative correlation by Colbert (1946, p. 267) in which the First Watchung, Second Watchung, and Hook Mountain extrusives of the upper Brunswick are shown as equivalents of the lower, middle, and upper lava flows of the Meriden

(the anterior, main, and posterior traps of earlier authors), while the rest of the upper and the middle Brunswick are equated to the New Haven arkose. It is (so far as the evidence goes) entirely in harmony with the occurrence of *Stegomus arcuatus* in the New Haven arkose at New Haven and in the lower Brunswick shales near Neshanic, New Jersey (Jepsen, 1948). But the pitfalls and complexities of Newarkian correlation are many and the evidence is still inadequate for a positive, much less a dogmatic, statement on the relative ages of these beds.

Even less adequate than the data for stratigraphic correlation is our information on the extinction of the chirotheriids and the subsequent fate of the ecological niches which they had occupied. The problems here are comparable in complexity to those involved in the extinction of the dinosaurs — with the additional handicap that our whole understanding of adaptive relationships must be derived primarily from the pedal structure, trunk and limb proportions, and gait of the animals as revealed in the trackways; and secondarily (subject to much doubt) from our knowledge of the fossil reptiles with which we correlate the trackways. Difficulties in interpretation should not, however, deter us from listing the facts now available.

Chirotheriid footprints of a highly modified type, associated with those of coelurosauroid dinosaurs, occur as high in the European middle Keuper as the *Semionotus*-sandstone of Franconia (Beurlen, 1950), a formation which appears to have its age equivalent in the Lockatong formation of New Jersey (Bock, 1952, p. 425 ff.). The only Keuper chirotheriids known from North America occur at two horizons of the upper Brunswick formation, several thousand meters above the underlying Lockatong. *Chirotherium lulli* is the youngest of these species, and if the intercontinental correlations are correct it is also the youngest chirotheriid yet known.

If, as argued above, the *Chirotherium*-bearing beds of the upper Brunswick are older than the *Chirotherium*-barren beds of the Meriden, then extinction or at least extermination of the Newark chirotheriids must have taken place late in Brunswick time. *Chirotherium lulli* would thus appear to be nearly if not actually a terminal member of the group.

The causes underlying the extinction of the Chirotheriidae, a wide-ranging pseudosuchian lineage which originated sometime in the Permo-Triassic and flourished from Bunter until late middle Keuper time, are unknown. Competition with increasingly numerous and

well-adapted dinosaurs has been suggested as a contributory factor (Peabody, 1948). The composition of Newarkian footprint faunas suggests to me that ecological replacement by better-adapted pseudosuchians may have been at least as influential. Of course I have no intention of drawing sweeping conclusions from such meager evidence, but propose rather to point out some facts which may be significant.

If any evolutionary trend can be said to characterize the Keuper chirotheriids it is the tendency toward elimination of the lateral propping function of the thumb-like fifth pes digit. The various means by which this end was approached or attained have been discussed on page 173. Such a shift from a pentadactyl pes with a lateral prop to an essentially tetradactyl pes with a postero-lateral digital "heel" must have had a high adaptive value to take place, for the most part independently, in so many different footprint species (each probably representing a reptilian genus).

Despite this modification the Newarkian chirotheriids were still osteologically pentadactyl, as were all the adequately known quadrupedal footprint genera of the New Jersey basin. In the Connecticut Valley basin, however, there were only three rare quadrupeds — *Shepardia*, *Sustenodactylus*, and *Arachnichnus* — which seem to have had a rudimentary but functional fifth pes digit. In all the other small pseudosuchioid footprint genera — *Batrachopus*, *Cheirotheroides*, *Palamopus*, *Exocampe*, *Orthodactylus*, and *Comptichnus* — the pes was functionally tetradactyl. Among these genera certain species of *Batrachopus*, *Palamopus*, *Exocampe*, and *Comptichnus* were decidedly similar to *Chirotherium lulli* in size and gait and in general body proportions as deduced from the trackways. What evidence there is suggests that they may have been its ecological equivalents.

Obviously it would be absurd to postulate and then account for a pattern of ecological replacement on the basis of footprints alone. Nevertheless, it is at least suggestive to observe that most of the pentadactyl-pes pseudosuchians of the Newarkian epoch seem to have evolved toward a functional pseudo-tetradactyly and then disappeared during Brunswick time; but the pseudosuchians with true functional tetradactyly are first seen in the Meriden and flourished in Portland time, persisting into the highest footprint-bearing beds of the Newark series.

NOTE ON NAMES OF BRITISH CHIROTHERIIDS

The name *Chirotherium beasleyi* was first proposed by Nopcsa (1923, p. 144) for the species known as "form L" in Beasley's terminology. Peabody (1948, p. 345) has through an oversight given the same name to the well-known small-manus chirotheriid designated as "A 4" by Beasley, a splendid trackway of which was described without name by Lomas (1908), and refigured by Soergel (1925, fig. 61) and Abel (1935, fig. 34) with the erroneous identification *Chirotherium storctonense*. In the absence of an available name for "A 4," Dr. Peabody has graciously delegated to me the necessary renaming of this form:

CHIROTHERIUM LOMASI Baird, nom. nov.

I designate as type the trackway of eight consecutive manus-pes sets described by Lomas, now in the Geology Department of the University of Liverpool (LU 8020). Specimens in this country include University of Cincinnati Museum 24831, a left pes; Yale Peabody Museum 3762, a right set; and Amherst College Geological Museum, Hitchcock cabinet 26/25, a right set and a manus from another trackway. The Amherst specimen has been figured by Lull, 1904 (pl. 72, figs. c-d) under the name *Chirotherium storctonensis*. This usage of Lull's was appropriate at the time, for "A 4" was not recognized as a form distinct from *C. storctonense* until 1906, when Beasley described it before the British Association at York (76th Report, p. 299).

SUMMARY

A trackway of four manus-pes sets from the Upper Triassic Brunswick formation of Milford, New Jersey, proves to be the counterpart of the type, a single set. This additional material shows *Chirotherium lulli* Bock to be a small, long-fingered member of the large-manus group of chirotheriids, primitive in many respects but specialized in the position and function of the thumb-like fifth pes digit. Affinities with ornithosuchid pseudosuchians are indicated by a skeletal restoration. Associated on the slab are two types of small tridactyl dinosaur footprint whose affinities, though uncertain, appear to lie with footprints from the Keuper of Pennsylvania.

Two American *Chirotherium*-dinosaur associations, from different horizons of the same formation and locality, are now on record.

The conspicuous absence of chirotheriids from the abundant Connecticut Valley footprint faunas, and the apparent lack of barriers between the New Jersey and Connecticut basins, suggest that the *Chirotherium* faunas in the Brunswick formation of New Jersey antedate the Meriden formation of Connecticut. *Chirotherium lulli*, the last known member of a widespread and long-ranging group of pentadactyl-pes pseudosuchian reptiles, appears to have been replaced ecologically by small, functionally tetradactyl-pes pseudosuchians such as *Batrachopus*.

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